

EXPERIMENTS ON POPULATION REGULATION IN TWO NORTH AMERICAN PARIDS

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Two major hypotheses to explain annual fluctuations of avian populations have emerged from long-term studies of the Great Tit (*Parus major*) in England (Perrins 1965, Lack 1966) and the Netherlands (Kluijver 1951, 1971; Kluijver and Tinbergen 1953). Lack (1966) argued that annual changes in Great Tit breeding populations reflected mortality of immatures due to starvation between leaving the nest and early winter, whereas Great Tit numbers in Holland according to Kluijver (1951, 1971) were regulated by a behaviorally induced emigration in fall rather than by direct starvation. Although natality often is variable in Great Tit populations from year to year, neither hypothesis considers variation in reproduction directly responsible for changes in breeding numbers. Nor does it appear that spring territory acts as a major density dependent factor regulating a population of the Great Tit (Krebs 1971) or of 2 other European parids, the Crested Tit (*P. cristatus*) and Willow Tit (*P. montanus*) (Cederholm and Ekman 1976), but controversy remains (Slagsvold 1975).

Although several North American parids have been intensively studied (Odum 1941, 1942; Dixon 1963; Smith 1972, 1976; Glase 1973), it remains unclear what factors influence annual changes in their numbers. The purpose of this study was to experimentally test Lack's and Kluijver's hypotheses on populations of the Black-capped Chickadee (*P. atricapillus*) and Tufted Titmouse (*P. bicolor*) in central Pennsylvania.

STUDY AREA AND METHODS

The study area of ca. 60 ha was centrally located in the 2800-ha Stone Valley Experimental Forest, Pennsylvania State University, 17 km southeast of State College, Huntingdon Co., Pennsylvania. The mature forest on the study area of black oak (*Quercus velutina*), white oak (*Q. alba*), red maple (*Acer rubrum*), white pine (*Pinus strobus*) and gray dogwood (*Cornus racemosa*) is interspersed with steep slopes, gullies and intermittent streams.

The 3 phases of the study were: (1) to describe under natural circumstances the location and size of breeding territories and winter flocks; (2) to test Lack's hypothesis by providing supplemental food from late summer through winter and observing responses of fall-winter flocks and subsequent breeding populations; and (3) to examine Kluijver's hypothesis by conducting a fall removal experiment and noting the timing and extent of recolonization.

During phase 1 from September 1974 through May 1975, 18 titmice and 26 chickadees were trapped and fitted with a USFWS numbered aluminum band. Thirteen titmice and

14 chickadees were marked with unique combinations of colored plastic leg bands. We used mist nets and 1-cell Potter traps baited with sunflower seeds to capture birds. Birds were sexed following Wood (1969) supported by our own measurements of 42 Black-capped Chickadee and 39 Tufted Titmouse museum specimens. Aging was by skull examination (Miller 1946). In addition to the banding records, we mapped all observations of color-marked birds to describe the spatial organization and membership of 3 winter chickadee flocks (designated BFL 1, BFL 2, and BFL 3) and 3 winter titmouse flocks (designated TFL 1, TFL 2, and TFL 3). Other flocks were located but 6 was the maximum that could be studied intensively. The number of breeding territories was estimated each spring by mapping singing males (Kendeigh 1944). From March to May we conducted 6 censuses in 1975, 7 in 1976 and 4 in 1977. Even though color-marked in fall and winter, females were difficult to observe in spring and were not always individually identified.

For phase 2, we fed mealworms (*Tenebrio* sp.) and sunflower seeds beginning in mid-July 1975. Mealworms were not consumed by the parids, but sunflower seeds were, starting in early September 1975. From this date to 1 March 1976, a feeder holding 11.3 kg of sunflower seeds, suspended by several fine wires or attached to a 3-m pole equipped with a squirrel guard, was placed within the range of flocks BFL 1, BFL 2, TFL 1, and TFL 2 as defined in the 1974–75 winter. Because of the overlap of BFL 1 and TFL 1, and BFL 2 and TFL 2, each flock had access to 2 feeders. Feeders were checked at least weekly and more frequently in cold weather. They were moved each week to a new location. Over 700 kg of sunflower seeds were fed to the parids and other species. Between September 1975 and April 1976, we placed USFWS bands on an additional 31 chickadees (27 color-marked) and 17 titmice (17 color-marked).

In phase 3 from September 1976 to January 1977 we bi-weekly removed all flock members that could be captured within a morning. Seven 1-cell Potter traps, usually baited on the preceding day but left locked open, were placed in an overlap of BFL 1 and TFL 1 and 6 within the ranges of BFL 2 and TFL 2. Trapped birds were marked and displaced 17 km. No titmouse or chickadee returned.

Availability of arthropod food for the Black-capped Chickadee and Tufted Titmouse during the breeding season was measured in a mature forest similar to Stone Valley 17 km northeast of the study area. Four sweep net (0.3 m diam.) samples of 50 sweeps each were taken in the shrub–lower canopy every 10 days from May into September 1976. These arthropods were frozen, dried at 50°C and weighed.

RESULTS

The 3 chickadee flocks marked in the fall and early winter of 1974 included 8 birds in BFL 1, 7 in BFL 2, and 8 in BFL 3. Membership in these flocks remained fairly constant from October through January with only 1 male in BFL 1 and 1 in BFL 2 disappearing in mid-winter. The ranges of the 3 flocks did not overlap (Fig. 1) except for 1 male of BFL 1 which was captured in all 3 flock ranges. Chickadees foraged in groups of 6 to 8 until late February when males began to establish territories. Four males from BFL 1 and 3 males from BFL 2 used nearly half of their respective winter flock ranges to establish breeding territories (Fig. 1). One of 4 males of BFL 3 defended a territory that extended beyond the BFL 3

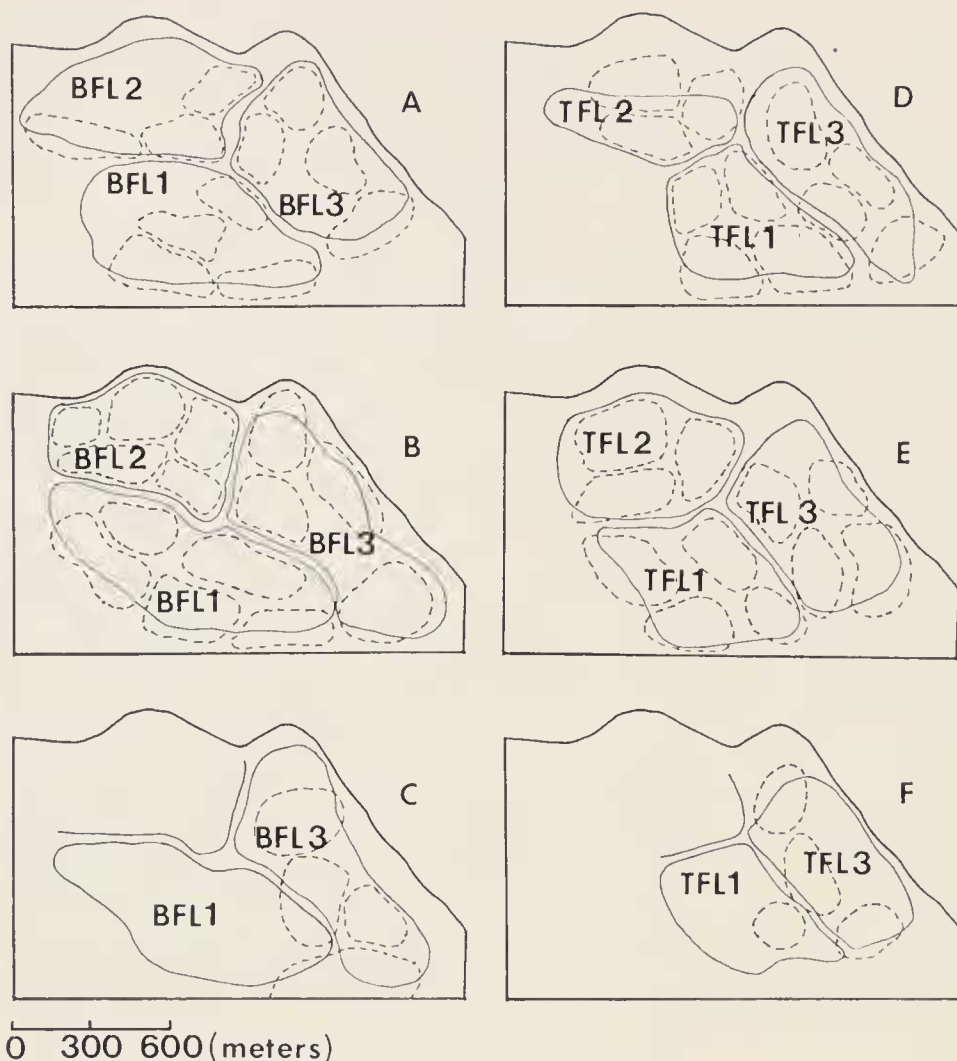


FIG. 1. Spatial arrangement of winter flocks and breeding territories of Black-capped Chickadee in: (A) winter-spring of 1974-75; (B) winter-spring of 1975-76; (C) winter-spring of 1976-77; and of Tufted Titmouse in: (D) winter-spring of 1974-75; (E) winter-spring of 1975-76; and (F) winter-spring of 1976-77. A winter flock range is outlined by a solid line and a breeding territory by a dashed line. Flock abbreviations (BFL 1, TFL 1, etc.) are defined in the text. Flocks BFL 1, BFL 2, TFL 1, and TFL 2 were experimental populations in 1975-76 and 1976-77 and BFL 3 and TFL 3 served as control populations.

winter flock range even though vacant habitat within the winter range was available.

Fig. 1 shows the spatial relationships of the 3 titmouse flocks in the winter of 1974-75. From October to mid-February, 7 birds were in TFL 1, 5 in TFL 2, and 8 in TFL 3. These flocks were mutually exclusive throughout the winter. Titmice most often foraged in groups of 2 or 3 but no group covered the entire flock range. In late February and early March, titmouse flocks broke up when males began to exhibit territorial behavior. Four males

from TFL 1 established territories that almost entirely overlapped with their winter flock range (Fig. 1). Similarly 3 males of TFL 2 created territories that included a major portion of their winter flock range. An unmarked male of unknown origin and 3 marked males of TFL 3 defended territories that included most of the TFL 3 winter range.

Fall-winter feeding experiments.—When testing Lack's hypothesis, Krebs (1971:14) pointed out that "if winter (supplemental) feeding had a measurable effect, the breeding density in the experimental area should have a larger increase relative to the control area." Supplemental feed (sunflower seeds) was provided to BFL 1 and BFL 2 and TFL 1 and TFL 2 from early September 1975 through late February 1976. This feeding ceased 1 March 1976 to prevent the acceleration of breeding caused by supplemental food as noted in the Great Tit (Källander 1974). BFL 3 and TFL 3 served as control flocks.

Both experimental chickadee flocks (BFL 1 and BFL 2) were larger as observed on 25 weekly censuses between 8 September 1975 and 6 March 1976, relative to the control flock BFL 3. BFL 1's flock size of 15 (8 in 1974-75) and BFL 2's of 13 (7 in 1974-75) were larger than the 8 for the control BFL 3 (8 in 1974-75). Four chickadees in BFL 1, 4 in BFL 2, and 4 in BFL 3 were banded in the preceding winter. Two first-year birds from BFL 2, 1 first-year bird from BFL 2, and 1 adult from BFL 3 disappeared during this winter.

In the spring of 1976, 4 males from BFL 3 established territories in a spatial arrangement similar to the preceding spring (Fig. 1). Five males of BFL 2 defended territories which included portions of the BFL 2 winter range vs 3 males in the 1975 spring. The breeding density in or near the winter range of BFL 1 increased from 4 males in the spring of 1975 to 5 in 1975.

Neither TFL 1 nor TFL 2 increased in number relative to the control TFL 3 during the supplemental feeding. TFL 1 as observed on 25 weekly censuses beginning 8 September consisted of 8 birds, TFL 2 had 8 and TFL 3 had 6 birds in the 1975-76 winter compared with 7, 5, and 8, respectively, for the 1974-75 winter. Five birds from TFL 1, 3 from TFL 2, and 3 from TFL 3 had been banded in the preceding winter. One female from TFL 2 and 1 male from TFL 3 disappeared during the winter. No major change was evident in the breeding density from 1975 to 1976 (Fig. 1). Similar to the preceding year, 4 males from TFL 1, 3 from TFL 2, and 4 from TFL 3 established territories that encompassed at least part of their respective winter flock range.

Fall removal experiments.—During the breeding season and after the spring migration, the experimental removal of established territorial males

TABLE 1
SUMMARY OF EXPERIMENTAL REMOVAL OF TUFTED TITMICE

Month	Flock 1		Flock 2	
	No. trap hours ¹	No. removed	No. trap hours ²	No. removed
Sept.	53.5	3 (1) ³	45.5	4 (1)
Oct.	95.0		80.9	3 (2)
Nov.	229.2	2	195.3	4 (3)
Dec.	90.2		76.8	
Jan.	100.0		85.3	
TOTAL	567.9	5 (1)	483.8	11 (6)

¹ Seven 1-cell Potter traps, includes time when removing birds from traps.

² Six 1-cell Potter traps, includes time when removing birds from traps.

³ Number of immatures in parentheses.

followed by their rapid replacement has been interpreted to show that territorial behavior limits a local population density (Watson and Moss 1970, Krebs 1971, Thompson 1977). If, as suggested by Kluijver (1951, 1971), tit populations are regulated by fall territorial behavior, birds removed from fall flocks should be replaced by individuals displaced by that or other intraspecific strife associated with dominance hierarchies. From September 1976 through January 1977, trapping efforts attempted to remove all chickadees and titmice from BFL 1, BFL 2, TFL 1, and TFL 2, respectively, while BFL 3 and TFL 3 served as controls.

Six Black-capped Chickadees from BFL 1 and 7 from BFL 2 were removed in September 1976. No additional chickadees were captured from October 1976 through January 1977 during 567.9 trap hours in the range of BFL 1 and 483.8 trap hours in the range of BFL 2. Three of 6 in BFL 1 and 3 of 7 in BFL 2 were juveniles. Two of 3 adults in BFL 1 and 3 of 3 in BFL 2 had been banded in a preceding winter. In the subsequent breeding season the number of males (4) establishing territories in BFL 3 remained constant from the preceding 2 springs, but no territories were established in the winter range of BFL 1 (vs 4 in 1975 and 5 in 1976). The range of BFL 2 was not censused.

Four of 5 tits removed from TFL 1 were more than 1 year old as were 5 of the 11 birds removed from TFL 2 (Table 1). Three of 4 adults in TFL 1 and 4 of 5 in TFL 2 were banded in a preceding winter. Only 1 titmouse established a territory in the range of TFL 1 (Fig. 1), vs. 4 in 1975 and 1976, but the range of TFL 2 was not censused. It is possible the male defending a territory in the range of TFL 1 was a member of TFL 3,

TABLE 2

MEAN DRY WEIGHT AND MEAN NUMBER OF ARTHROPODS PER MONTH COLLECTED
IN SWEEP NET SAMPLES AT APPROXIMATELY 10-DAY INTERVALS FROM
5 MAY TO 20 SEPTEMBER 1976

Month		Dry weight (g)		Number	
		\bar{x}	SD	\bar{x}	SD
May	(12) ¹	0.094	0.065	33.8	11.8
June	(12)	0.087	0.046	36.0	10.0
July	(12)	0.145	0.108	33.8	3.8
Aug.	(8)	0.059	0.029	36.9	8.6
Sept.	(8)	0.076	0.036	64.8	12.5

¹ Number of 50-sweep samples per month in parentheses.

but tits rarely descended below 15 m during the breeding season, making individual recognition difficult. Three males in 1977, as compared to 4 in 1976, defended breeding territories in TFL 3.

Food resources.—Table 2 summarizes the dry weight and number of arthropods collected at approximately 10-day intervals from 5 May to 20 September 1976. There was no significant difference in mean weight among the 5 sample periods (2-way ANOVA, $F = 1.44$). The heaviest samples were collected in late July and early August with a substantial decline in biomass during late August and early September. Numbers of arthropods per 50 sweep samples varied greatly because of change in numbers of small Diptera and arachnids collected in some samples.

DISCUSSION

Two major questions in avian population ecology revolve around the timing and extent of mortality in relation to annual fluctuation in breeding numbers and the existence or non-existence of surplus individuals that are prevented from breeding by fall or spring territorial behavior. Lack (1966:75) contended that "annual fluctuations in the breeding populations of the Great Tit in Marley Wood were due primarily to corresponding variations in juvenile mortality before winter" with most occurring within 2 or 3 weeks of leaving the nest. Perrins (1965) provided indirect evidence supporting Lack by showing that lighter juvenile Great Tits in England apparently had lower survival rates than heavier juveniles. However, Kluijver (1966), in an experimental test of Great Tit density and early post-fledging mortality, did not support the conclusions of Lack and Perrins.

He removed 60% of the eggs of a Great Tit population breeding on the isolated Dutch North Sea island of Vlieland, yet this did not affect the subsequent breeding density (Kluijver 1966, Klomp 1972).

We were not able to examine mortality during the 2 or 3 week post-fledging interval. Broods of chickadees and titmice fledged on the study area from mid-June to mid-July. Neither species exhibited the drastic decrease in height of feeding (to the level of the feeders) observed in Great Tits by Royama (1970) when young were fledged. Several factors, however, suggest juvenile mortality was minimal on the study area during this interval. In the summers of 1975 and 1976, family groups varied little in size in both species and were observed through July and August, although adults were particularly aggressive toward young in late August and September. In both chickadee and titmouse flocks in the fall of 1976, our banding indicated juveniles outnumbered adults. In the 1976 summer, arthropod biomass remained high until late August and a similar pattern presumably existed in 1975. Good juvenile survival into August has been reported in Black-capped Chickadee populations by Odum (1942), Smith (1967) and Glase (1973) but little information exists for this interval in the Tufted Titmouse (Dixon 1955, Brackbill 1970).

The role of mortality and dispersal in determining population size in late summer or fall has been considered by several authors (Snow 1958, Jenkins et al. 1963, Tompa 1964, Southern 1970). Lack (1966:79) reported a strong correlation between tit numbers and size of a fall "beechmast crop" even though the mast was available well after the post-fledging period. He further pointed out that this relationship existed in areas without beech but with other trees producing seeds in the same years as beech. Artificial winter feeding of Black-capped Chickadee flocks can be associated with increased winter numbers (Wallace 1941, Hamerstrom 1942, Odum 1942, this study). There are additional suggestions, particularly in finches and sparrows, that winter food supply is important in determining numbers of breeding birds (Newton 1964, Fretwell 1969, Pulliam and Enders 1971). However, to date the only experimental test of the effect of fall-winter food on subsequent breeding numbers is by Krebs (1971).

In Krebs' (1971) study, the numbers of Blue Tit (*P. caeruleus*) (but not Great Tit) breeding pairs per ha increased following the supplemental feeding of sunflower seeds from 1 October 1968 to 22 April 1969. He suggested 3 possible reasons Blue Tit breeding density increased after feeding: (1) food directly influenced territory size, (2) feeding increased winter survival, (3) immigration occurred from surrounding areas. We ceased feeding when vernal territorial behavior was first observed, to prevent food serving as a proximate factor influencing territorial establish-

ment or to accelerate the onset of breeding. Feeders also were moved each week to reduce any effect of the location of feeding stations on territorial arrangements. Flock size of both species remained nearly constant from mid- or late October to February in the control year (1974–75) as well as in the control and experimental flocks in 1975–76. Smith (1967) also reported good overwinter survival in Black-capped Chickadees, and Glase (1973:241) noted that “with the exception of the disappearance of certain individuals in late August and early September, the composition of flocks found in mid-August remained constant throughout the rest of the flocking period.” In the Plain Titmouse (*P. inornatus*), Dixon (1949) reported 11 of 14 (78.5%) pairs re-mated for at least 1 season which suggests a good winter survival. Condee (1970), in a winter study of the Tufted Titmouse, reported considerable movement and consistent clan (perhaps family groups) membership through a winter, but did not directly discuss survival. Rather than food serving as a proximate factor in improving winter survival, it appears to influence the degree of immigration.

Whether juvenile chickadees banded in September or October 1975 were raised by pairs breeding on the study area is not known. The fall ratio of juveniles to adults in experimental flocks increased from 1:1 in BFL 1 in 1975 to 2.75:1 in 1976, and from 0.75:1 on BFL 2 in 1975 to 2.3:1 in 1976, suggesting either a reduced dispersal or increased immigration. Although supplemental feeding on BFL 1 and BFL 2 increased winter numbers of chickadees 87.5% (8 to 15) and 85.7% (7 to 13), respectively, breeding density increased only 25% (4 to 5) and 66% (3 to 5). It is not clear why the increase in breeding density did not parallel the increased winter flock size; those marked males failing to obtain a territory were not observed again. Smith (1967:357) described a “sharply defined period of high mortality, emigration, or both” when flocks break up and territorial behavior begins in spring and a similar pattern appeared to exist in our experimental chickadee populations.

Watson and Jenkins (1968), in a series of carefully designed autumn removal experiments, reported that breeding numbers of Red Grouse (= Willow Ptarmigan) (*Lagopus lagopus*) are influenced by territorial behavior in the preceding fall. When a territorial male was removed in fall, he was rapidly replaced. However, if removed in spring, males were replaced rarely or not at all, since surplus cocks die during late autumn and winter. Other experimental evidence based on removal experiments to explain the effect of fall territory on breeding numbers is lacking, even though the removal procedure has been used to define the effect of spring territory on breeding numbers (Orians 1961, Bendell and Elliott 1967, Krebs 1971, Zwickel 1972, Bendell et al. 1972, Samson 1976, Thompson 1977).

In this study, we planned to remove all individuals of both species every 2 weeks to determine if replacement would occur in either species and to ascertain the size and sex, and age structure of any replacement population. All chickadees were removed on 13 and 19 September from BFL 1 and BFL 2, and they were not replaced. Other species, including 6 White-breasted Nuthatches (*Sitta carolinensis*), were caught in November within BFL 1's range. In BFL 2's range, 3 White-breasted Nuthatches, 5 Downy Woodpeckers (*Picoides pubescens*) and 1 Blue Jay (*Cyanocitta cristata*) were caught in November. This trapping and our previous success in capturing chickadees and titmice suggest our trapping techniques were unable to detect subsequent replacements.

Condee (1970) reported that Tufted Titmice in winter in central Pennsylvania formed clans of 3 to 6 individuals. Each clan had a winter territory and, although some overlap was evident, there were no conflicts reported. Also in Pennsylvania, Gillespie (1930) reported winter groups of 2 to 6 titmice with nearly exclusive ranges and Nee (1933) reported winter flocks with definite ranges. Van Tyne (1948) and Dixon (1955) reported that titmouse flocks may consist of 1 or more pairs although a pair may only occasionally be a member of a flock. Our observations agree with Van Tyne and Dixon even though no pair traversed our entire flock winter range.

In removing titmice, 7 (TFL 1) or 6 (TFL 2) traps were all located within a 15 m radius and not necessarily within the range of a group of tits. This may have influenced the pattern of removal involving a 6-week period in TFL 1. The origin of the 1 adult and 3 young removed in November from the range of TFL 2 is not known and they may have been replacements. It is also possible that the unmarked adult replaced a breeder from TFL 2 and raised the young within the range of TFL 2.

The level of replacement noted in removal experiments conducted in spring on other species, however, was not evident in either chickadee or titmouse flock ranges. Examples include the rapid replacement of 27 of 28 (96.4%) Great Tits removed by Krebs (1971), 211 (approximately) of 204 (103.4%) Blue Grouse (*Dendragapus obscurus*) by Zwickel et al. (1972), and 27 of 40 (67.5%) male Yellow-breasted Chats (*Icteria virens*) by Thompson (1977). In the cases of the Great Tit and chat, the authors provide convincing evidence of nearby territory holders expanding holdings, re-occupying abandoned territories, or moving from marginal to more favorable habitat, with little or no evidence for the existence of a surplus or non-breeding population. Our fall removal experiments also indicate the non-existence of surplus flocks and, more importantly, that winter flock size and the subsequent breeding density appeared to be established by the

preceding fall. They do not fully clarify the role of intraspecific strife in autumn, for it may have had a major impact on the emigration and mortality before the onset of our experimental removals.

Summarizing, if one removes birds in mid-September there are no chickadee and few titmouse replacements. Thus, there appears to be an interval of dispersal prior to or during late August and early September followed by considerable mortality or decreased movement (i.e., no recolonization). This dispersal in 1976 preceded the decrease in food as measured by arthropod biomass. In nearly all cases those surviving this interval were able to attempt to breed the subsequent spring. Thus, Lack's (1966) hypothesis that a period of mortality accompanying the decline in summer food sources influences subsequent breeding densities may explain the lack of replacements in this study, but we have no proof of individual mortality. Whether, as suggested by Kluijver (1951, 1971), intraspecific strife in autumn has a major impact on emigration and mortality needs further investigation, principally through removal experiments beginning before early to mid-August when food decreases and aggressive behavior increases.

SUMMARY

Black-capped Chickadees in fall formed flocks that were nearly exclusive in membership. At end of winter, flocks broke up when males established territories. Similarly, Tufted Titmice in fall formed flocks that remained together through winter, yet no pair traversed the entire flock range. Black-capped Chickadees, but not Tufted Titmice, responded to supplemental feeding with a substantial increase in fall-winter flock size but only a minor increase in breeding density. Replacement following fall removal experiments did not occur in the Black-capped Chickadee and was limited in the Tufted Titmouse. We interpret these results as possible support of Lack's hypothesis for regulation of an avian population, but they did not resolve the role of late summer-autumn intraspecific strife in regulation of a parid population as suggested by Kluijver.

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